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Abstract

The influence of temperature (17, 21, 25, 30 and 35°C) on life history traits of a Q-biotype *Bemisia tabaci* population on tomato is studied. Temperature dependent relationships are characterized for immature developmental rate, immature survival, fecundity, longevity and intrinsic rate of increase. Development time vary from 20 days at 30°C to 56 days at 17°C and the lowest thermal threshold is estimated at 10.2°C. The optimal temperature for immature development is 32.5°C. Total fecundity (eggs per female) ranges from 105.3 (at 21°C) to 41 (at 35°C). The longevity decreases with temperature increase. The intrinsic rate of increase ranges from 0.0450 (at 17°C) to 0.123 (at 30°C). The functional relationships between temperature and life-history parameters are used to evaluate the effect of temperature on the population dynamics. Such mathematical relationships could provide a basis for future development of population models.

Key words

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Temperature, bionomics, *Bemisia tabaci*, Q biotype, modelling

**Introduction**

The sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is one of the most serious agricultural pest on tomato *Lycopersicum esculentum* (Mill) and other horticultural crops in tropical and subtropical temperature regions worldwide. Damage may be caused directly by feeding on phloem or deposition of honeydew, or indirectly by transmitting different types of plant viruses, such as the tomato yellow leaf curl virus (Oliveira *et al.*, 2001), to a wide range of vegetable crops. The potential of *B. tabaci* to develop resistance in response to intensive use of pesticides has led to studies on integrated pest management strategies in which biological control plays a central role, and significant advances have been made in developing and implementing management systems (Gerling & Mayer, 1996; Naranjo, 2001). As a general rule, any pest management programme should be based on adequate knowledge of the main factors responsible for changes in population dynamics. Life history parameters estimated under different biotic or abiotic conditions provide the basic tools for among others, understanding changes in the status of pest species (Poole, 1974; Dempster, 1975; Krebs, 1978; Southwood, 1978). Because *B. tabaci* is a poikilothermic organism i.e. temperature influences the life table components, it is important to take this factor into consideration in explaining population ecology. A review by Drost *et al.* (1998) reported that biological parameters of *B. tabaci* have been characterized for different temperatures, host plants and biotypes. Among this vast amount of literature, the most complete work is probably that of Wang & Tsai (1996) concerning B-biotype reared on aubergine.
The Q-biotype of B. tabaci was first characterized in samples collected in the south of Spain and Portugal (Guiro et al., 1997). Successive surveys showed that this biotype is also present in Tunisia (Chermitti et al., 1997), Morocco (Monci et al., 2000), Egypt (De Barro et al., 2000), Israel (Horowitz et al. 2003) and southern Italy (Demichelis et al., 2000; Simón et al., 2003). Because of its high degree of polyphagy and its ability to transmit a relatively wide range of plant viruses, the Q-biotype is considered as a particularly dangerous biotype (Muñiz, 2000; Navas-Castillo et al., 2000). In spite of the wide distribution of the Q-biotype in the Mediterranean basin, no complete published work is available currently on its life-history parameters in relation to temperature when reared on tomato. The aim of the present study was to characterize and analyze functional relationships between temperature and life-history parameters and to evaluate the effect of temperature on the dynamics of Q-biotype populations.

Materials and methods

Whitefly source and host plant production

In 2002, founders of Bemisia tabaci of the Q biotype were collected from a greenhouse of tomato crop located in Alenya in the South of France (42°38’N; 2°58’E). The stock colony was reared and maintained on tomato plants of the cv Hilario® (Royal Sluis, Enkhuizen, The Netherlands) in plastic cages placed in climatic chambers at 25 ± 1°C, and 60 ± 5% RH. Experiments were carried out using progeny after more than 3 generations on Hilario.
Development of immatures

Young adults of B. tabaci (150 pairs: male and female) were placed in cubic screened cages (50 x 50 x 50cm) each containing a young potted tomato plant. The cages containing adults were maintained in a growth chamber at 25 ± 1°C, 60 ± 5% RH in a LD 14:10 h photocycle. Whitefly adults were given 3 h to lay eggs. The adults were then removed, leaves were observed under a stereo-microscope at 36X magnification. Two eggs on the abaxial surface of 5 leaves were kept and excess eggs were killed using an insect pin. Plants were then placed in growth chambers set at 5 constant temperatures: 17, 21, 25, 30 and 35°C with six replicates. Once the eggs hatched and the crawlers fixed on the leaf, young nymphs were identified individually. Each nymph was observed daily until adult emergence, and the transition from one stage to another was noted. Differences between developmental times were tested by one-way ANOVA and means were separated by Newman–Keuls test (α=0.05). Statistical analyses were performed using XLStat 7.1 (Addinsoft). The influence of temperature (T) on developmental rate was described by the model proposed by Logan et al. (1976):

\[
DR = \frac{1}{p_1} \times \left[ \exp \left( p_2 \times (T - T_i) \right) - \exp \left( p_2 \times (T_m - T_i) - \left( \frac{1}{p_3} \right) \times (T_m - T) \right) \right]
\]

where \(DR\) is the development rate which is the reciprocal of development time, \(T_i\) is the lower temperature tested and \(T_m\) is the upper threshold derived from the observations. The parameters, \(p_1\), \(p_2\) and \(p_3\) were estimated by regression. The lowest thermal threshold for development (LTT) was calculated by the ratio: \(LTT = \frac{a}{b}\), \(a\), \(b\) were determined by linear regression of the equation \(DR = a + bT\), for temperature (\(T\)) interval over which the relation was linear.
Differences between survival rates were tested using $\chi^2$ test ($\alpha=0.05$). The relationship between temperature ($T$) and immature survival rate was described by the Curry & Feldman (1987) model:

$$SI = \frac{\left( (T + 273) \times \exp \left( p1 - \left( \frac{p2}{(T + 273)} \right) \right) \right)}{\left[ 1 + \exp \left( p3 + \left( \frac{p4}{(T + 273)} \right) \right) + \exp \left( p5 - \left( \frac{p6}{(T + 273)} \right) \right) \right]}$$

Where $SI$ is survival of immatures, $T$ is temperature in °C, and $p1$ to $p6$ are regression coefficients.

Reproductive capacity and female longevity

One newly emerged (<24 h) female and two males were placed in a clip-cage on the abaxial surface of new leaflets. For each temperature tested, 30 clip-cages were kept in growth chambers (60±1% RH, LD 14:10h photocycle). The clip-cages with insects were moved to new leaves daily and the number of eggs laid per female was counted until death of the female. Differences in fecundity and female longevity were compared with ANOVA followed by a Newman–Keuls tests ($\alpha=0.05$). Exponential functions were used to describe the influence of temperature on total fecundity and longevity.

Fecundity:

$$EN = p1 \times \left[ (T^{p2}) \times \exp \left( p3 \times T \right) \right]$$
Where $EN$ is total number of eggs laid per female; $T$ is temperature in °C; and $p1$, $p2$, $p3$ are regression coefficients.

Longevity:

\[ L = \exp [p1 + p2 \times T] \]

Where $L$ is longevity per female in days; $T$ is temperature in °C; and $p1$, $p2$: are regression coefficients.

**Demographic parameters**

The net reproductive rate ($R_0$), the mean generation time ($G$), the intrinsic rate of natural increase ($r_m$) and the finite rate of increase ($\lambda$) were determined using the program developed by Hulting *et al.* (1990) in which the parameters are calculated using the method recommended by Birch (1948). The program, based on Jacknife's procedures, gives a variance and hence a standard error to each parameter calculated enabling statistical comparison of values (Meyer, 1986). The relationship between $r_m$ and temperature was also described using the Logan *et al.* (1976) model (see above).

**Results**

**Development of immatures**
*B. tabaci* required 56 days at 17°C to complete its development from egg to adult, but only 20 days at 35°C (Table 1). Between 17 and 30°C, the developmental time was negatively correlated with temperature, but no significant difference was found between 30 and 35°C (*P* > 0.05). Values of Logan equation parameters were *p*1 = 0.0115, *p*2 = 0.0921, *p*3 = 0.3133 (*R²* = 0.92, *P* < 0.01). Between 17 and 30°C, the relation was linear and the *LTT* was estimated at 10.2°C (Fig. 1). The optimal temperature for development, calculated from the derivative Logan equation, was 32.5°C.

Survival rates at 21, 25 and 30°C (Table 2) were not significantly different (*χ²* = 0.695, *P* = 0.707) even if the highest percentage was measured at 25°C. Temperature of 17°C had the greatest effect on immature development especially in the 4th stadium. The curve obtained by fitting the Curry & Feldman model to the data (*p*1 = -6.55, *p*2 = -200.18, *p*3 = -2986.08, *p*4 = 865870, *p*5 = 1353.19, *p*6 = 6417118, *R²* = 0.99, *P* < 0.01) described the influence of temperature very well and indicated that 17 and 35°C were close to the lower and upper thermal limits, respectively (Fig. 2).

**Longevity and reproductive capacity of females**

Temperature had a significant effect on the fecundity and longevity of females. Longevity was negatively correlated with temperature. The longest life was recorded at 17°C and the shortest at 35°C (Table 3). The pre-oviposition period was very short (less than 24h) for almost all females tested and oviposition period was close to longevity for the 5 temperatures tested. The relation between temperature and female longevity (Fig. 3) was very well described by the exponential function (*p*1 = 5.02, *p*2 = -0.079, *R²* = 0.99, *P* < 0.01).
Except for 17°C, fecundity followed the same trend as longevity, i.e., was negatively correlated with temperature. Figure 4 shows the influence of temperature on fecundity ($p1=9.9\times10^{-11}$, $p2=12.8$, $p3=0.54$, $R^2=0.89$, $P<0.01$). Our results showed that optimal fecundity was obtained from temperatures ranging between 21 and 25°C. The sex-ratio calculated for each treatment was not significantly different than 50% ($P>0.05$).

Demographic parameters

Parameters were calculated with the sex-ratio of $B.\ tabaci$ set to 0.5. At the five temperatures tested, the highest rate of increase ($r_m$) was obtained at 30°C and the lowest at 17°C (Table 4). At 25, 30 and 35°C, the rates of increase were not significantly different ($P>0.05$). The net reproductive rate was lower at 17°C and 35°C indicating the proximity of lower and upper thermal thresholds, respectively.

The curve (Fig.5) obtained by fitting the Logan model ($p1=0.019$, $p2=0.099$, $p3=0.331$, $R^2=0.99$, $P<0.01$) describes the influence of temperature on the rate of natural increase very well. The optimal temperature for population development, calculated from the derivative Logan equation was 31.3°C.

Discussion

Based on biological and ecological information published in the two last decades, the immature developmental time of $B.\ tabaci$ (from egg to adult) depends on the host plant (Coudriet et al., 1985; Van Lenteren & Noldus, 1990; Bethke et al., 1991; Zalom et al., 1995; Tsai & Wang, 1996; Muñiz & Nombela, 1997; Nava-Camberos et al., 2001) as well as on the whitefly populations or biotypes (Drost et al., 1998; Muñiz, 2000; Muñiz & Nombela, 2001). The developmental time of $B.\ tabaci$
recorded at 25°C ranges from 17.3 to 22.8 days when reared on either aubergine, tomato, sweet potato, cucumber, bean or pepper. The present results show that on tomato, the population of Q-biotype *B. tabaci* newly introduced in southern France require 25.6 days to complete development from egg to adult at 25°C. In contrast, Tsai & Wang (1996) report a shorter developmental time (17.96 days) for a Floridian *B. argentifolii* population on tomato (cultivar Suny Hybrid) at 25°C. Based on the model of Logan et al. (1976), the optimal temperature for the development of immatures (32.5°C) is higher than that calculated for Florida, Mississipi, and Arizona populations of *B. argentifolii* (29.9, 28.2, and 30.0°C, respectively) on aubergine (Wang & Tsai, 1996). The optimum for *B. tabaci* biotypes on all host plants tested ranges from 30 to 33°C (Drost et al., 1998). The developmental threshold for immatures belonging to the population studied here, estimated at 10.2°C, is lower than that reported in the literature, which ranges from 10.8°C (Von Arx et al., 1983) to 12.5°C (Wang & Tsai, 1996).

Based on the range of temperatures tested here, survival rates of immature stages of *B. tabaci* from egg to adult are higher on the tomato cultivar Hilario than those reported on other cultivars of tomato (Tsai & Wang, 1996), Poinsettia (Enkegaard, 1993) and cotton (Wagner, 1995). Different responses to extreme temperatures, i.e. in mortality of immatures, suggest that the Q-biotype population on tomato is more tolerant to high temperatures (>33°C) than diverse *B. tabaci* populations on aubergine (Wang & Tsai, 1996), cotton, and Poinsettia (Drost et al., 1998).

Fecundity of *B. tabaci* is generally highly variable and depends on temperature (Enkegaard, 1993), host-plant species (Liu & Oetting, 1994), and cultivar (Navon et al., 1991). Thus, the total number of eggs laid at 25°C by a Q-biotype female reared on tomato cv Hilario (94.2 eggs) is considerably lower than that reported in the
literature for females reared on aubergine (223.67) (Wang & Tsai, 1996) and tomato cv Suny Hybrid (165.55) (Tsai & Wang, 1996).

Wang & Tsai (1996) underline the importance of life table parameters to compare *B. tabaci* populations and biotypes. On aubergine these authors (Wang & Tsai, 1996) find a high intrinsic rate of increase at 25°C (0.192), 27°C (0.191), and 30°C (0.169) compared with that found with the Q-biotype population on tomato at 25°C (0.106) and 30°C (0.123). However, at 35°C, the net rate of increase of the B-biotype (0.073) is lower than that of the French Q-biotype population (0.104). The tolerance to extreme thermal conditions of the population newly introduced in France is also confirmed by its shortest mean generation time recorded at 35°C (24.6 days).

The comparison between the results of this work and those from other studies (Wang & Tsai, 1996; Muñiz & Nombela, 1996, 2001; Drost *et al.*, 1998; Nombela *et al.*, 2000, Muñiz, 2000) demonstrates clearly that the relationship between life-history parameters and temperature is influenced highly by both insect biotype and host plant species and variety. In spite of this high degree of variability within the *Bemisia* complex, it is essential to better understand the population dynamics of the newly introduced pest population in relation to temperature to improve control strategies and evaluate its geographical extension capacity.

**References**


Table 1. Developmental period (day ± SE) of immature stages of *Bemisia tabaci* (Q biotype) at 5 constant temperatures.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>n</th>
<th>eggs</th>
<th>instar 1</th>
<th>instar 2</th>
<th>instar 3</th>
<th>instar 4</th>
<th>From egg to adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>80</td>
<td>21.5±0.09a</td>
<td>9.4±0.35a</td>
<td>7.5±0.93a</td>
<td>8.0±0.42a</td>
<td>9.4±0.33a</td>
<td>55.8±0.47a</td>
</tr>
<tr>
<td>21</td>
<td>80</td>
<td>14.0±0.09b</td>
<td>7.1±0.21b</td>
<td>4.1±0.18b</td>
<td>8.8±0.23a</td>
<td>5.6±0.18b</td>
<td>39.6±0.69b</td>
</tr>
<tr>
<td>25</td>
<td>80</td>
<td>10.4±0.13c</td>
<td>4.3±0.19c</td>
<td>3.7±0.16bc</td>
<td>3.8±0.15b</td>
<td>3.4±0.12c</td>
<td>25.6±0.26c</td>
</tr>
<tr>
<td>30</td>
<td>80</td>
<td>7.7±0.06d</td>
<td>3.2±0.13d</td>
<td>3.3±0.15c</td>
<td>3.5±0.15b</td>
<td>2.5±0.09d</td>
<td>20.2±0.24d</td>
</tr>
<tr>
<td>35</td>
<td>38</td>
<td>6.5±0.10e</td>
<td>3.9±0.17cd</td>
<td>3.3±0.21c</td>
<td>3.5±0.29b</td>
<td>3.3±0.22c</td>
<td>20.5±0.33d</td>
</tr>
</tbody>
</table>

Within columns means followed by the same letters are not significantly different (P>0.05).
Table 2. Survivorship (percentage) of immature stages of *Bemisia tabaci* (Q biotype) at 5 constant temperatures.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>n eggs</th>
<th>egg</th>
<th>instar 1</th>
<th>instar 2</th>
<th>instar 3</th>
<th>instar 4</th>
<th>n adults</th>
<th>From egg to adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>80</td>
<td>91.3</td>
<td>84.9</td>
<td>96.8</td>
<td>73.3</td>
<td>63.6</td>
<td>38</td>
<td>48c</td>
</tr>
<tr>
<td>21</td>
<td>80</td>
<td>98.7</td>
<td>98.7</td>
<td>93.4</td>
<td>93.0</td>
<td>97.0</td>
<td>64</td>
<td>83a</td>
</tr>
<tr>
<td>25</td>
<td>80</td>
<td>100</td>
<td>93.8</td>
<td>94.7</td>
<td>98.6</td>
<td>97.1</td>
<td>68</td>
<td>85a</td>
</tr>
<tr>
<td>30</td>
<td>80</td>
<td>100</td>
<td>95.0</td>
<td>96.1</td>
<td>93.2</td>
<td>97.1</td>
<td>66</td>
<td>82a</td>
</tr>
<tr>
<td>35</td>
<td>38</td>
<td>100</td>
<td>97.4</td>
<td>89.2</td>
<td>78.8</td>
<td>92.3</td>
<td>24</td>
<td>63b</td>
</tr>
</tbody>
</table>

Within columns means followed by the same letters are not significantly different (P>0.05).
### Table 3

Fecundity (number of eggs per female ± SE) and longevity (days ± SE) of *Bemisia tabaci* (Q biotype) at 5 constant temperatures.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>n</th>
<th>Total fecundity</th>
<th>Longevity</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>30</td>
<td>49.3 ± 6.7b</td>
<td>39.6 ± 3.6a</td>
</tr>
<tr>
<td>21</td>
<td>30</td>
<td>105.3 ± 10.4a</td>
<td>27.3 ± 0.8b</td>
</tr>
<tr>
<td>25</td>
<td>30</td>
<td>94.2 ± 12.3a</td>
<td>21.9 ± 1.7c</td>
</tr>
<tr>
<td>30</td>
<td>30</td>
<td>58.6 ± 10.4b</td>
<td>14.6 ± 1.1d</td>
</tr>
<tr>
<td>35</td>
<td>30</td>
<td>41.0 ± 5.6b</td>
<td>8.5 ± 0.7e</td>
</tr>
</tbody>
</table>

Within columns means followed by the same letters are not significantly different (P>0.05).
Table 4. Comparison of life table parameters of *Bemisia tabaci* (Q biotype) at 5 constant temperatures. n = number of females. $r_m$ = Jacknife estimate of the intrinsic rate of increase. CI= confidence interval estimate of $r_m$. Ro = net reproductive rate (Standar error). G= mean generation time in day. $\lambda$= finite rate of increase $= \exp(r_m)$.

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>Parameters</th>
<th>n</th>
<th>$r_m$</th>
<th>95%CI</th>
<th>Ro</th>
<th>G</th>
<th>$\lambda$</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td></td>
<td>30</td>
<td>0.045c</td>
<td>0.044-0.046</td>
<td>29.8 (0.2)</td>
<td>77.2</td>
<td>1.05</td>
</tr>
<tr>
<td>21</td>
<td></td>
<td>24</td>
<td>0.079b</td>
<td>0.078-0.080</td>
<td>52.5 (0.1)</td>
<td>49.9</td>
<td>1.08</td>
</tr>
<tr>
<td>25</td>
<td></td>
<td>18</td>
<td>0.106a</td>
<td>0.090-0.121</td>
<td>39.5 (5.5)</td>
<td>35.1</td>
<td>1.11</td>
</tr>
<tr>
<td>30</td>
<td></td>
<td>24</td>
<td>0.123a</td>
<td>0.103-0.142</td>
<td>23.6 (4.3)</td>
<td>26.5</td>
<td>1.13</td>
</tr>
<tr>
<td>35</td>
<td></td>
<td>23</td>
<td>0.104a</td>
<td>0.087-0.119</td>
<td>12.3 (1.8)</td>
<td>24.6</td>
<td>1.11</td>
</tr>
</tbody>
</table>

Within columns means followed by the same letters are not significantly different (P>0.05).
Figure captions

Fig. 1. Influence of temperature on development time of Bemisia tabaci (Q biotype). Points: experimental values. curve simulated by Logan et al. (1976).

Fig. 2. Influence of temperature on survivorship of Bemisia tabaci (Q biotype). Points: experimental values. curve simulated by Curry & Feldman model (1987)

Fig. 3. Influence of temperature on female longevity of Bemisia tabaci (Q biotype). Points: experimental values. curve simulated by exponential model.

Fig. 4. Influence of temperature on fecundity of Bemisia tabaci (Q biotype). Points: experimental values. curve simulated by multiplicative exponential model.

Fig. 5. Influence of temperature on intrinsic rate of increase of Bemisia tabaci (Q biotype). Points: experimental values. curve simulated by Logan et al. (1976) model.
Fig. 1.
Fig. 2.

![Graph showing temperature vs. survival percentage.](image-url)
Fig. 3
Fig. 4.
Fig. 5.